THE INSECTS OF BRITISH TREES: COMMUNITY EQUILIBRATION IN ECOLOGICAL TIME[1]

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Abstract

The most widely accepted model of insect-plant interaction derives from the correlation between insect species richness and the relative number of recorded Quaternary fossil remains of British tree species (Southwood, 1961). The implications of this relationship are: 1) that community formation and the equilibration of insect species richness is a very slow process, taking at least 2 million years, 2) that introduced plant species will necessarily have relatively few associated insect species, 3) that insect communities are basically different from vertebrate communities in that saturation of species does not occur (Whittaker, 1969).

I present a model mutually exclusive to Southwood's, indicating that insects of British trees follow a species area relationship. The implications of this new finding are: 1) insect community formation and equilibration of species richness occurs at least within 300 years, 2) the insect diversity of introduced plants becomes a function mainly of the range of distribution of the plant within ecological time, 3) insect communities do not differ from vertebrate communities in terms of species saturation rate. The saturation occurs within ecological time for both groups.

Plant/insect interactions are apposite to general ecological thought because they provide the only uncontested example of non-equilibrium community biology; the number of insect species associated with tree species apparently can increase continually and without limit over long periods of geological time. This is suggested by Southwood (1961), who shows the number of insect species recorded from British trees to be positively and linearly correlated with the total number of Quaternary fossil records of the tree taxon. This implies community formation and any resultant equilibration of species number for these insects to be a very slow process, taking longer than the Quaternary or between 15,000 and 2 million years—depending upon "one of the most popular topics in all biogeography . . . . whether the whole fauna and flora of the British Isles immigrated in post-glacial times, or whether some fraction survived from an earlier time" (Deevey, 1949). Extremely protracted community development is logically necessary given the fact that there is no asymptote in Southwood's correlation and that native trees are on the same line as species introduced only 300 years ago. The Oaks provide a good example. *Quercus petraea* and *Q. robur* are native species that together have the richest associated insect fauna of any tree taxon in Great Britain (284 species), whereas *Quercus ilex*, introduced into Britain about 400 years ago has only 2 associated insect species. Southwood's correlation predicts that after another 14,600 to 2 million years in Britain *Q. ilex* will have many more species of insects associated with it, however by that time *Q. petraea* and *Q. robur* will also have acquired many more. But unless the relative abundance or distributions of these two taxa change, the difference between them in number

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[1] I thank Tom Ray for counting the 60 thousand-odd dots in Perring and Walters for this study.

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of associated insect species will remain constant. The non-asymptotic nature of the correlation implies that the rate of addition of insect species to the fauna of a tree taxon is independent of the number of insects already in that fauna. Perhaps within another million years, "saturation" (MacArthur, 1965) or "equilibrium" (MacArthur & Wilson, 1963) will have occurred for the insect biotas of the oldest or most perenially abundant tree species, and continued existence in the flora will not add any more insect species to their faunae. However Southwood's correlation gives no indication that these faunae will ever saturate. The correlation supports Whittaker's contention that similar generalizations may not apply to insect and bird communities: "Bird communities can thus be saturated, determinate in their evolution of diversity; but plant and insect communities may show indefinite, indeterminate evolutionary increase in diversity" (Whittaker, 1969).

However there is a problem with Southwood's correlation. It ignores the influence of present abundance of host taxa upon associated insect species richness. The general importance of present conditions in determining diversity has been well established by the species-area relationship. For many taxocenes of birds, reptiles, phanerogams, and invertebrates the number of species in a biota is a function of the present area supporting the biota, when geographically close and similar areas are considered. (See Simberloff, 1972, for review.) This relationship, $S = kA^z$ (Preston, 1960) where S = number of species, A = area of the region considered, k = a constant for the biota in question, and z = ratio of log species addition per log area addition, has been most often demonstrated to explain the difference in richness among the biotas of oceanic islands, but there is no reason that it should not be valid for "islands" on the mainland as well. Indeed, Janzen (1968) has suggested that host plants are islands in a sea of vegetation for phytophagous insects. Hence I reason that for the British insect/tree system the analogue of area, of "A" in the species-area relationship, should be the present range or breadth of distribution of a host tree taxon.

The idea that cumulative ancient host tree abundance determines species richness of associated insect faunae is an extension of the popular notion that the antiquity of a biota determines its species richness (Wallace, 1878; Wimpenny, 1941; Dunbar, 1960; Fischer, 1960; Zenkevitch, 1961; Sanders, 1968). This "geological time theory" of organic diversity proposes that the number of species in a biota tends to grow steadily through long periods of geological time. It is obvious that geological time theories and recent or ecological time theories are competing or alternative explanations of species richness. That a biotas's antiquity determines its species richness is in conflict with the idea that ecological conditions during recent times control richness. However both may operate, one being a major factor and the other being minor, or both may be of relatively equal importance, or finally one of the two may be shown to be overwhelmingly more important in determining species richness. By subtracting the amount of variation in insect richness attributable to variation in present day range from the total amount of insect richness variation it is possible to establish the proportion contributed by cumulative ancient abundance of the host taxon.

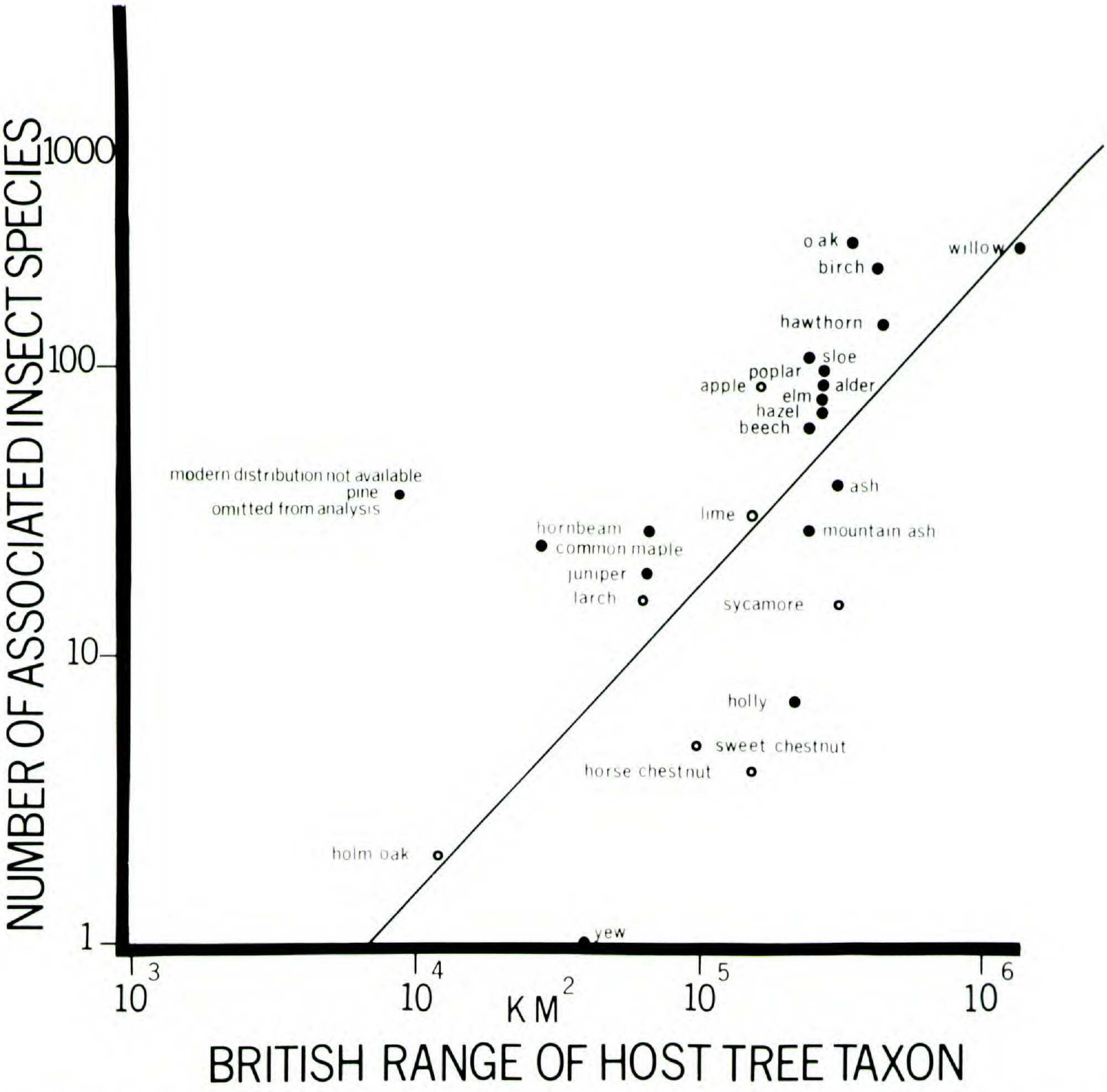

FIGURE 1. The number of insect species associated with British tree taxa, as a function of the present-day range in Britain of the tree taxa (Perring & Walters, 1962). Native species are indicated by closed points, introduced species by open circles. Apple is a mixed taxon, with both native and introduced elements in Britain. The slope of the regression line = 1.10. The correlation coefficient = .78, $p < .001$. The datum for pine is its inferred native range, Perring and Walters do not give its present distribution.

In Figure 1 I show the strong relationship between insect species richness and the present day range of British tree species. The host tree range data are taken from the dot maps of the *Atlas of the British Flora* (Perring & Walters, 1962). I used all modern records of host distribution from this source. Unfortunately the distributions of 4 tree species treated by Southwood's correlation are not given by Perring and Walters. I have included all host tree taxa for which there is distributional informaton in Perring and Walters. I computed the range of each host taxon as the sum of the ranges of sub-taxa listed in Perring and Walters. Some of these hosts are not taxonomically subdivided in Perring and Walters (*e.g. Corylus*, *Taxus*, *Fraxinus*, etc.) and others are (*e.g. Salix* with 18

TABLE 1. Data of origin, number of associated insect species, and present range of British tree taxa. The information of tree origin and associated insect species richness is from Southwood (1961), that for range of the tree taxa is from Perring and Walters (1962). For pine, only data of inferred "native" distribution are available; Perring and Walters do not give the modern distribution of this species.

Tree Taxon	Status	Number of associated insect species	Present range × 10 km²
Quercus petraea & *robur* (oak)	Native	284	3593
Betula spp. (birch)	"	229	4217
Corylus avellana (hazel)	"	73	2885
Salix spp. (willow)	"	266	14,358
Alnus glutinosa (alder)	"	90	2931
Crataegus spp. (hawthorn)	"	149	4648
Fraxinus excelsior (ash)	"	41	3187
Pinus sylvestris (pine)	"	91	38 "native" range
Ilex aquifolium (holly)	"	7	2388
Taxus baccata (yew)	"	1	326
Prunus spinosa (sloe)	"	109	2564
Populus spp. (poplar)	"	97	2834
Ulmus spp. (elm)	"	82	2984
Fagus sylvatica (beech)	"	64	2639
Acer campestre (common maple)	"	26	277
Carpinus betulus (horn beam)	"	28	683
Juniperus communis (juniper)	"	20	624
Tilia spp. (lime)	"	31	1634
Sorbus aucuparia (mountain ash)	"	28	2446
Castanea sativa (sweet chestnut)	Introduced, 100 A.D.	5	986
Malus spp. (apple)	Native & introduced	93	1651
Qeurcus ilex (holm oak)	Introduced, 1580	2	129
Larix decidua (larch)	Introduced, 1629	17	608
Aesculus hippocastaneum (horse chestnut)	Introduced, ca. 1600	4	1692
Acer pseudoplatanus (sycamore)	Introduced, ca. 1250	15	3097

spp.). The insect data are from Southwood (1961). The data are given in Table 1.

Figure 1 shows a significant species-area relationship ($r = .78$, $p < .001$), hence broadly distributed tree taxa have more associated insect species than do narrowly restricted ones, and a new and very different interpretation from that forced by the Southwood correlation is needed. The most important change in thinking necessitated by Figure 1 is that the diversity of insect/host plant systems must now be regarded as asymptotic; the breadth of geographic distribution of British tree taxa sets an upper limit to the number of associated insect species, and the faunae of most if not all of the analyzed tree taxa are at that upper limit.

The regression of Figure 1 gives an indication of how rapidly the asymptote in species number (the saturation or equilibrium level) is reached. There are

5 introduced taxa in the analysis (sweet chestnut, holm oak, larch, horse chestnut, and sycamore) and two taxa of mixed (introduced and native) origin, apple and lime. There is no tendancy for the introduced taxa to fall below the regression line, which would be the case if the introduced (younger) host taxa were not yet saturated with insect species. Three of the introduced taxa are below the line and three are above. I have included lime as an introduced taxon, as most of its distributional records are contributed by native specimens; apple is not included as most of its distributional records are contributed by natives (Perring & Walters, 1962). A more powerful demonstration that the introduced species do not tend to fall below, or the natives above, the regression line is given by the non-parametric *Wilcoxon Two Sample Rank Test* of the regression residuals; the hypothesis that the residuals of introduced taxa are distributed about the regression line differently than are the natives is rejected by this test ($p > .14$, n.s., with both lime and apple included among the introduced taxa; $p > .12$, n.s. with lime but not apple included among the introduced species; $p > .05$, n.s. with neither apple nor lime included among the introduced species). Because introduced species do not fall below the regression line the asymptote for this system is reached in less than 350 years, as larch was introduced into Britain in 1629 (Southwood, 1961). A further example of how rapidly the equilibrium is reached is given by the case of pine, *Pinus sylvestris*. This tree is very widely distributed throughout the British Isles, but records are only available for the presumed "native distribution" of the species. Apparently British botanists feel its present distribution to be somehow irrelevant because this distribution is the result of man's activities. The number of associated insects shows the present, albeit anthropochorous, distribution to be highly relevant ecologically (Fig. 1). There are enough insect species associated with pine in Britain to allow it a range much broader than its native one. Most of the change in distribution of pine has probably been within the last 500 years, therefore the adjustment of insect species richness has also been within this period. This rapidity of accumulation of insect species on plant species suggests that instead of host transference of an insect species being a rare event Zwölfer & Harris, 1971), it is rather a common event that classical entomological methods rarely detect.

Though this analysis of the simple species-area regression strongly suggests that present distribution of host trees is by far the most important determinant of the number of species of associated insects, it has not ruled out the possibility that there is some small contribution to this richness from age and/or ancient abundance of the host taxon. I have tested this with multiple regression. With this technique one can assign proportional contributions to the variation of the dependent variable by the independent variables. The results of multiple regression of $\log_{10}$ number of insect species upon the independent variables "$\log_{10}$ host range" and "number of Quaternary remains" for each host taxon are given in Table 2. The meaning of the results is clear; although the fossil data does not add significant explanation of the variance in insect species number when $\log_{10}$ host range is the first variable treated by the analysis, $\log_{10}$ of host range does add significant explanation of the variance in insect species number when the

TABLE 2. Analysis of variance of multiple regression of range and number of fossil records upon associated insect species richness of British tree taxa.

Log$_{10}$ S Regressed on Log$_{10}$ Range of Host Taxon, and Number of Fossil Records

SOURCE	D.F.	MEAN SQUARE	F
Due to regression	2	3.03	15.78 $p < .001$
Added by fossil record	1	.58	3.01 n.s.
Deviation about regression	21	.19	

Log$_{10}$ S Regressed on Log$_{10}$ Host Taxon Range, and Log$_{10}$ Number of Fossil Records

SOURCE	D.F.	MEAN SQUARE	F
Due to regression	2	3.07	16.40 $p < .001$
Added by log$_{10}$ fossil record	1	.67	3.58 n.s.
Deviation about regression	21	.18	

Log$_{10}$ S Regressed on Number of Fossil Records, and Log$_{10}$ Host Taxon Range

SOURCE	D.F.	MEAN SQUARE	F
Due to regression	2	3.03	15.78 $p < .001$
Added by log$_{10}$ range	1	2.38	12.43 $p < .001$
Deviation about regression	21	.19	

Log$_{10}$ S Regressed on Log$_{10}$ Number of Fossil Records, and Log$_{10}$ Host Taxon Range

SOURCE	D.F.	MEAN SQUARE	F
Due to regression	2	3.07	16.40 $p < .001$
Added by log$_{10}$ range	1	2.58	13.79 $p < .001$
Deviation about regression	21	.18	

fossil data is the first variable treated in the analysis. This tends to rule out the geologic history of the host as having a significant effect upon the number of insect species associated with these tree taxa.

The objection might be raised that, since geological record insect species richness correlations are significant, the geological record explains as much of the variance in insect species richness as does host plant range. This is a statistical quibble, naïve of the biology of the system, and is incorrect for three reasons: 1) species-area relationships are known to be almost ubiquitously important in determining species richness, hence any other factors have to be weighed after the species-area effect has been accounted for. 2) My statistical analysis of the regression residuals of introduced *versus* native species, and my multiple regression analysis show cumulative ancient abundance of host taxa to have insignificant effect upon the insect species richness in comparison to host plant ranges. 3) The logic of the matter precludes giving fossil records of very different ages equivalent weight in the analysis as Southwood (1961) has. Figure 2 shows a hypothetical but not unrealistic diagram of fossil abundance of a host tree taxon as a function of the age of these fossils. Southwood's correlation would assign equal weight to records at the right- and left-hand end of the graph. The intermediate periods of lack of abundance of this hypothetical tree taxon would tend to lead to the extinction of associated insect species. There are many dramatic peaks and valleys in the actual fossil record diagrams of the host tree taxa (Godwin, 1956). If one argues that these are not the result of fluctuations in abundance but rather of differential fossilization or discovery rates among the host

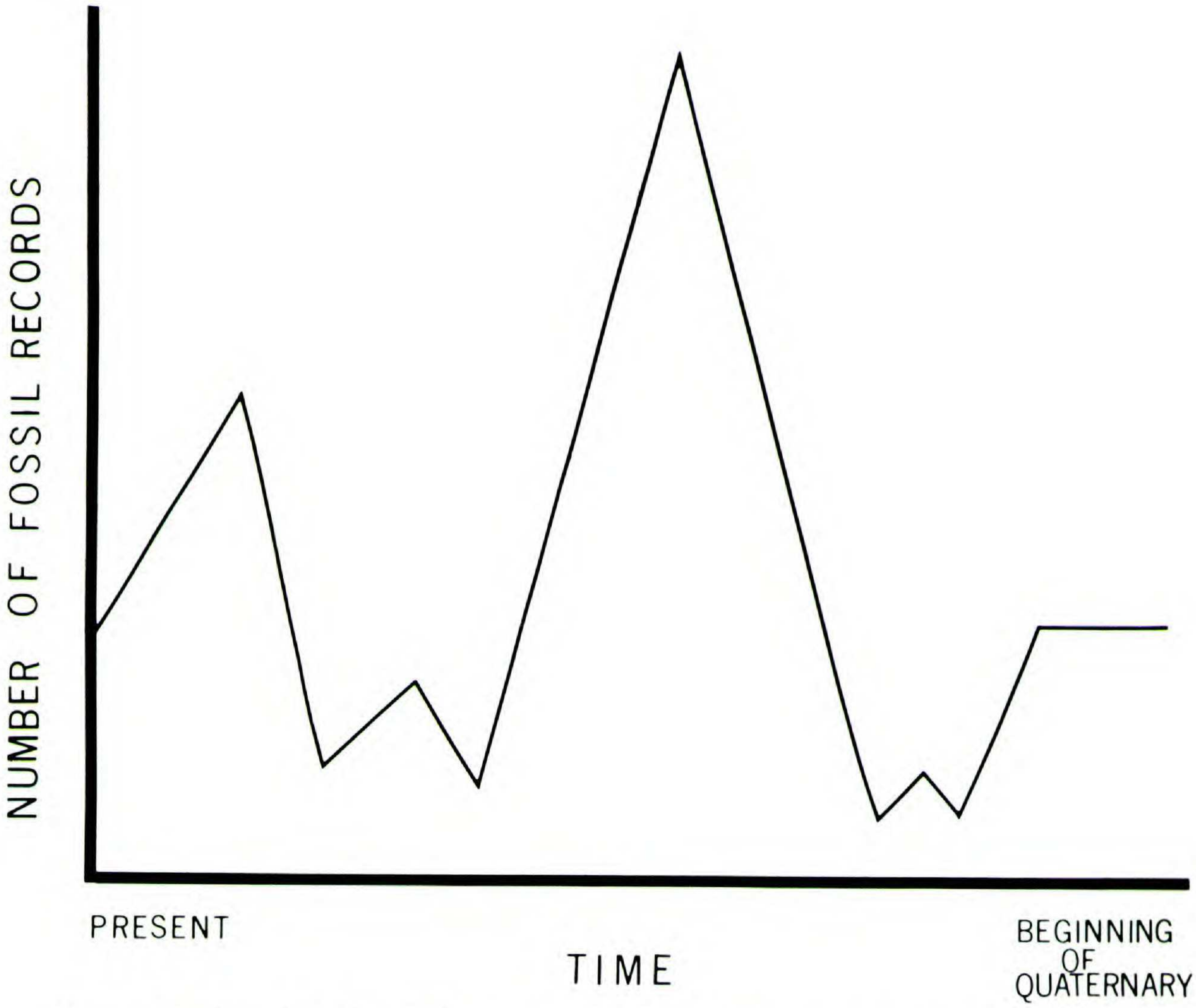

FIGURE 2. A graph of fossil discoveries as a function of age for a hypothetical host tree taxon. The cumulative number of Quaternary records for this taxon is the area under the curve. It is unreasonable to assume ancient and recent host tree abundance to contribute equally to extant insect species richness, because intervening periods of low abundance would lead to insect species extinction.

tree taxa, the entire basis of Southwood's correlation is vitiated; for his correlation to be causal, and not spurious, different numbers of fossil discoveries among the host taxa have to be an accurate history of relative abundance of once-living tree taxa. Carried to the extreme, the equal weighting of old and young fossil records is analogous to arguing that extinct plant species should have a number of extant associated insect species proportional to cumulative host plant abundance before extinction.

The above reasoning leads us to suspect that Southwood's correlation is fortuitous, highly unlikely but adventitious. The probability that this could happen is small but real (his $r = .85$, $p < .001$). It is likely that a contribution to this spurious correlation comes from the correlation between the number of fossil records of tree taxa and their present range. Figure 3 shows this relationship ($r = .53$, $p < .01$). I must stress that this does not compromise my earlier conclusion; causality of associated insect species richness derives from recent host plant range. Because the relative range of these trees has apparently not changed radically during the Quaternary in Britain the number of fossil records is correlated

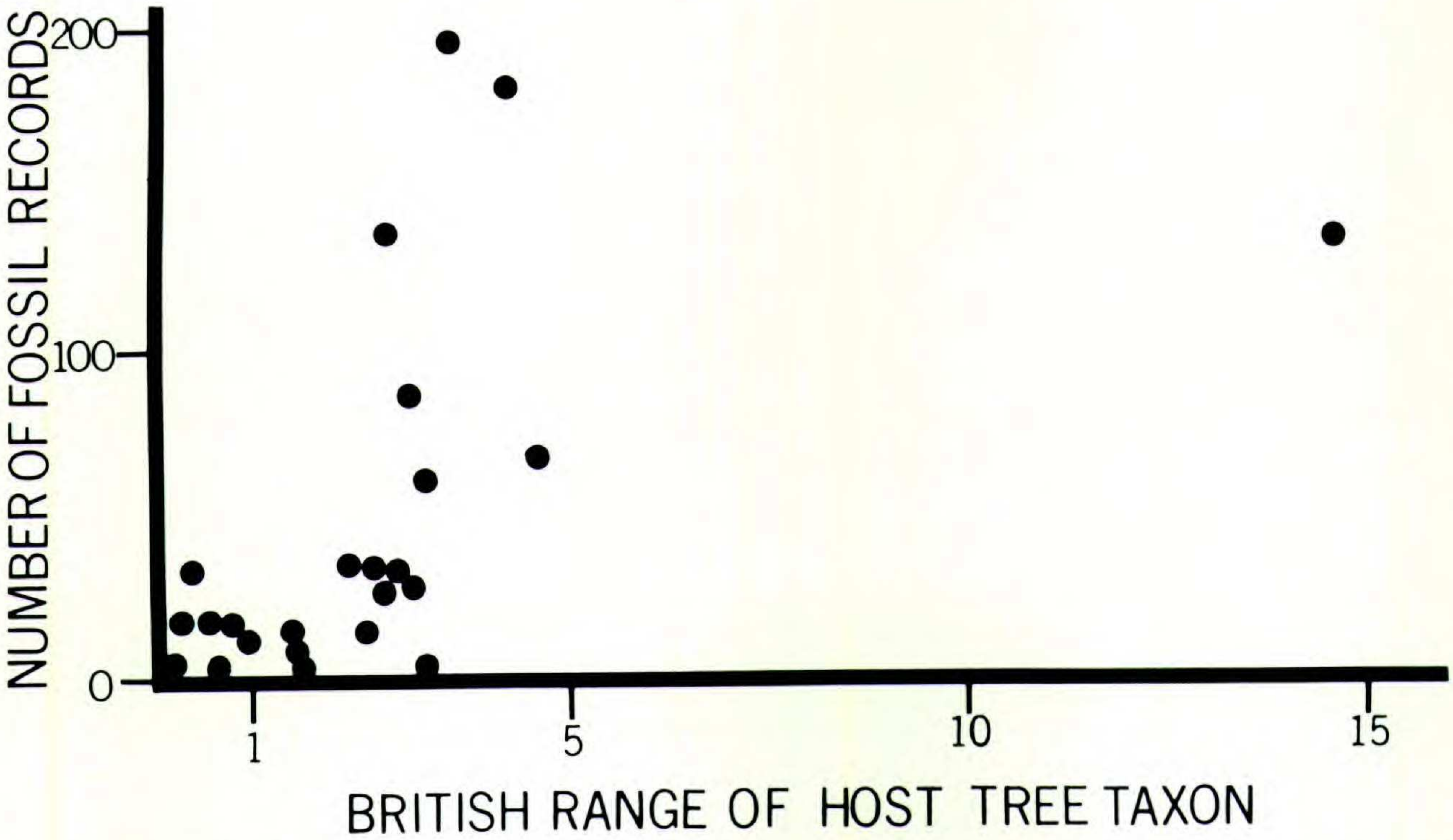

FIGURE 3. The number of fossil records of British tree taxa (Godwin, 1956) as a function of the present range of British tree taxa (Perring & Walters, 1962). The correlation is marginally significant ($r = .53$, $.01 > p > .001$). This correlation may contribute to the spurious correlation between the number of fossil records and the number of associated insect species of British trees (Southwood, 1961).

with range, hence number of fossil records is also correlated with the associated insect species richness. But the cumulative ancient host plant abundance does not cause the present day insect richness.

This system is different from the polynesian ant fauna (Wilson & Taylor, 1967) in that no secondary increase in species richness can be demonstrated after the species asymptote is first reached. The first equilibrium or saturation occurs within a few hundred years (perhaps much sooner?) for insects on British trees, and no discernable increase in richness follows. The conclusion of Ricklefs and Cox (1972), from Southwood's correlation, that "a history of abundance creates the opportunity for specialization" (leading to increased diversity) must then be withdrawn. Whittaker's (1969) idea that insect and bird communities are different, in that insect communities do not saturate whereas bird communities do, is incorrect as well. The British insect/tree information is the best data available, and the analyses in this paper indicate the saturation processes and rates to be strikingly similar for birds and insects.

This demonstration that insect species richness is a species-area phenomenon, independent of the effects of ancient host plant abundance and only a function of host range in ecological time, confirms MacArthur's (1965) suspicion of Southwood's correlation. MacArthur felt that the apparently non-asymptotic species accumulation suggested by the correlation could actually be asymptotic because "a single tree constitutes more than one habitat" (MacArthur, 1965: 518). This does not seem to be the reason however. The insect species asymptote is set by the geographic range of the host plant.

There are two possible mechanisms causing this species-area phenomenon, the number of distinct environments inhabited by the host species increases with range (Johnson & Raven 1973) and the effective population sizes of the insect species increase also with host range (Simberloff, 1973). Hence both increased habitat diversity and lowered insect species extinction rates may occur with greater host plant range. The only work to date that explores the role of decrease in extinction rate with increasing population size has been done with only very small islands, hence with only small populations (Simberloff, unpublished). Whether this extinction factor is significant over a range of "island sizes" as great as that covered by the ranges of the trees of Britain is questionable. It is probably more reasonable to consider each tree taxon as an archipelago than an island, because of the tremendous amount of discontinuity that must exist among trees, groves, and forests as well as among taxonomic subdivisions within the tree taxa. Given distributional discontinuities in host plant range, insect population sizes would not be as large as the entire range of the host, and insect species extinction rates would be expected to increase as a result. But on the other hand the discontinuities would cause isolation of subpopulations of the insect species, and sources of extinction that were contagious (disease, competition, heavy predation) would be prevented from spreading to effect the entire species.

The slope of the species-area regression line is equal to 1.1. This is the greatest slope ever reported for a species-area phenomenon. One explanation of this extreme value suggests itself—the data may be systematically biased to produce an overestimate of the slope. If the distribution of the more restricted host species were systematically overestimated and the distribution of the more wide ranging were systematically underestimated, the resultant slope would be an overestimate of the actual species-area slope. This type of bias is likely, given the nature of the data. Perring and Walters give only species presence or absence per 10 km^2; species with a single individual would be recognized as having a distribution not different from a species made up a solid forest 10 km^2. The other end of the host plant distributional range spectrum might also be biased by the data in Perring and Walters to overestimate the slope. Very broadly distributed trees perhaps are more dense where they do occur than are narrowly restricted species; this would give the species with greater range fewer dots per individual tree than narrowly restricted host taxa.

Finally it should be recognized that Southwood has proposed that both cumulative ancient abundance *and* present host plant distribution determine species richness of insects associated with trees; he has not proposed that the cumulative ancient abundance of host plants alone determines associated insect species number. He has pointed out that the relative abundance of Hawaiian tree species accounts for much of the variation in the species richness of their insect faunae (Southwood, 1960) and that a tree species will have a longer list of associated insect species in a country in which it is more abundant (Southwood, 1961). He however has never attempted to assess the relative magnitude of the contributions to associated insect species richness of the two factors. More important, he did not recognize that if the greatest contribution of this species richness were from cumulative ancient abundance, as his widely quoted correlation implies, the number of species in the system would not equilibrate and there would be no asymptote in species number through time. My analysis has established the system to be asymptotic by demonstrating the variation in insect species richness among tree taxa to be accounted for by a species-area phenomenon and by showing the contribution to the variation in insect species richness from cumulative ancient abundance of host tree taxa to be insignificant.

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